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LONG-TERM NATURAL HISTORY
SOME ASPECTS OF THE ENVIRONMENT AND LIVING THINGS

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Our new president, Roger Downie, in his earlier guise as Editor of the most recent issue of 'The Glasgow Naturalist' commented in his editorial that the Society rarely engages with major modern advances in the biological sciences and he posed the question: 'Is our Society taking too narrow a view of what natural history is?' Whilst not proposing to answer this question in full I propose to take a brief look at some controversial aspects of the subject that draws us all to this Society.

Natural history has been defined as the study of natural phenomena ....including inanimate phenomena, such as rocks, soils and climate, but commonly confined to living things, animals and plants in the wild. (Fitter, 1967). Ecology is defined as the study of the relationship between plants and animals and their environment. (Haeckel, biologist and philosopher, 1866).

I should like to look at the connection between these two in the light of present day knowledge. This means that I shall look at the inter-relationships between the environment, plants (mainly trees) and animals (mainly birds and mammals) with particular but not exclusive reference to a Scottish context.

My interest in atmospheric CO_2 concentrations goes back to science lab experiments carried out to compare the O_2, CO_2 and N_2 volumes of inhaled air with exhaled air. The CO_2 content of inhaled air, 370 ppm, is so small as to be immeasurable in the context of an ordinary laboratory. There is some 40 times more water vapour in the air than CO_2 and it is a matter of common observation that cloudy evenings are warmer than clear evenings. So simple logic suggests that small variations in atmospheric CO_2 concentration will have little effect on global temperature. This is very much at odds with what we come across in the media.

EARTH'S CLIMATIC HISTORY: THE LAST 1,000,000 YEARS

Some 10 major ice ages have occurred over the past 1 million years (Figure 1). They recur at approximately 100,000 year intervals, persist for about 90,000 years, after which they have been followed by approximately 10,000 year interglacials. This periodicity has been attributed to the Croll - Milankovitch cycle

(Figure 2), whereby regular changes in the distance of the earth from the sun affect the amount of solar radiation reaching the earth's surface (Farrow, 2001).

The glacial epoch about which we know the most is the most recent one which was at its peak about 20,000 years ago. Land plants suffered as the air's CO_2 content fell to about 180 ppm. This fall was caused by: a) the increased ability of colder water to hold more dissolved CO_2 and b) larger growth rates of phytoplankton caused by the amount of iron rich dust carried by the stronger winds of the period. Had the CO_2 concentration dropped much lower it is likely that several plant extinctions would have occurred, since many plants find it difficult to survive at CO_2 concentrations of the order of 50 to 100 ppm (Idso, 1989; Salisbury and Ross, 1978).

Large and rapid shifts in climate have been detected in Greenland and Antarctica from deep sediment cores, ice cores, lake sediments and pollen series, e.g. in Greenland rapid warming of some 7°C in a few decades was observed about 11,500 years ago (Dansgaard *et al.*, 1989; Johnsen *et al.*, 1992; Grootes *et al.*, 1993). Rapid warming, followed by periods of slower cooling and then rapid freezing are typical of interstadial events (as well as interglacials), of which about 20 occurred during the last glacial period. They lasted between 500 and 2000 years (Dansgaard *et al.*, 1993).

CO_2 AND TEMPERATURE: ICE CORE CORRELATIONS (Fischer *et al.*, 1999)

Evidence from Antarctic ice cores through the last three ice ages showed that the earth warmed up well before there was any increase in the air's CO_2 content. The relationship between temperature and CO_2 is just the reverse of what is assumed in all the climate model studies that warn of dramatic warming in response to the ongoing rise in the air's CO_2 content: temperature rises first, and then comes an increase in atmospheric CO_2.

NEARLY HALF A MILLION YEARS OF CLIMATE AND CO_2 (Petit *et al.*, 1999)

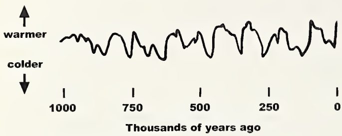
Petit *et al.*(1999) showed from the Vostok ice core going back 420,000 years that the 4 interglacials preceding the present one (the Holocene) were warmer by an average temperature of > 2°C. Hence the current interglacial is by far the coolest of the five most recent such periods (Figure 1).

Also "during glacial inceptio the CO_2 decrease lags the temperature decrease by several thousand years.". Since the current interglacial is by far the longest stable warm period of the past 420,000 years we are probably overdue for the next ice age.

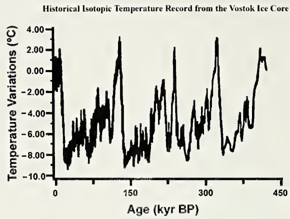
AIR TEMPERATURE OF THE PAST DECADE

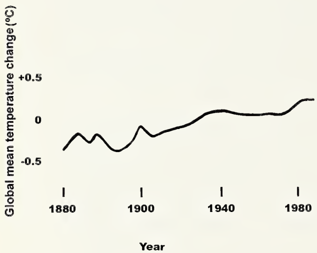
The air temperature of the last decade of the 20th century in terms of typical interglacial temperatures is clearly unusually cool, even if the temperature is warmer than it has been over the past 100 years (Figure 1). The air's CO_2 concentration today

Figure 1. Temperature change vs Time



Source: Budiansky, 1995





Source: Budiansky, 1995

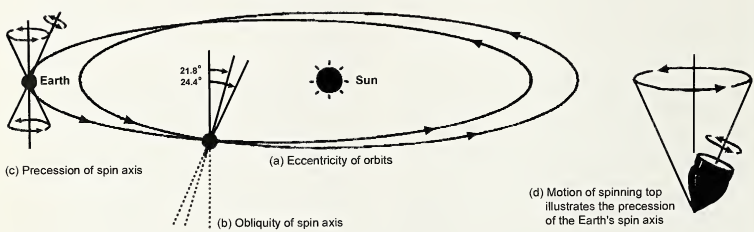
Regular patterns appear only on time scales of 100,000 years or more.

Top: Temperatures inferred from oxygen isotope fluctuations in ocean sediments.

Mid: From oxygen isotopes in the Vostok ice core.

Bottom: Global mean temperature from direct measurement.

Figure 2. Croll-Milankovitch Cycle



Earth's orbit varies in three ways: a), b) & c). These affect amount of radiation and so climate

Source: Lamb & Sington, 1999

stands at nearly 370 ppm whereas in the 4 prior interglacials it never rose above 290 ppm. So the higher temperatures of previous interglacials cannot be attributed to either CO_2 concentrations (they were lower) or to human interference (too few humans). So what is the most likely cause of climate change?

A 1000 YEAR HISTORY OF SUNSPOT NUMBERS (Rigozo *et al.*, 2001)

Both the Mediaeval and Modern maxima in sunspot numbers and solar radiation output are far above all other periods of the past thousand years. On this basis current temperatures are expected to be higher than at any other time during the past millennium. Studies of recent data from the European Space Agency's sun watching Soho satellite indicate a solar energy surge and a particularly big increase in UV light. This has coincided with a doubling in the strength of the sun's magnetic field, which blocks cloud-forming cosmic rays. Fewer clouds would mean that more heat reaches the Earth's surface, although it could be argued that warming of the Arctic Ocean has resulted in increased cloudiness at high northern latitudes. There is however no need to invoke variations in the air's CO_2 content as a cause of temperature variation.

ICE SHEETS IN THE NORTHERN HEMISPHERE (Figure 3)

When the ice of the last glaciation was at its greatest extent it reached south to the Chiltern hills, to the south and west of which was glacial outwash and tundra (Figure 4). The area south and west of Cornwall was dry land and may have been a refuge for trees such as the Strawberry tree (*Arbutus unedo*) which possibly migrated to southwest Ireland as the ice melted (Mitchell & Coombes, 1998). The ice of the last glaciation began to melt about 17,900 years ago (Huntley *et al.*, 1997) when the exposed land was colonised firstly by open ground taxa. These were then replaced by a dwarf shrub community that included *Juniperus, Salix* and *Betula nana* and occasional tree birches (Ramsay & Dickson, 1997). By about 14,600 years ago the ice had almost disappeared completely but by 12,900 year ago a substantial ice sheet, the Loch Lomond readvance, centred on Rannoch Moor had accumulated. About 11,200 years ago extremely rapid climatic warming caused the ice to melt finally thus allowing dwarf shrubs to migrate again into the area behind the melting ice. These were gradually followed by the major tree taxa.

After late-glacial times the first tree pioneers were the downy and silver birches (*Betula pubescens* and *B. pendula*) and Scots pine (*Pinus sylvestris*). The pollen record suggests that birch spread from the east across land now forming the bed of the North Sea. The genetic evidence is strong for the colonisation of Scotland by Scots pine by migration from north-central Europe mainly and from southern Europe (Ennos *et al.*, 1997). The expansion of pine from sheltered pockets in north west Scotland where it may have survived the last glacial period remains a matter of debate. In Scotland the tree birches were followed soon by hazel (Figure 5) then elm. Oak tends to arrive either at the same time as elm or slightly later (Ramsay & Dickson, 1997). Pollen analysis cannot distinguish between the two native oaks but the present distribution, with the sessile oak predominant in the north and west and at higher altitudes, suggest that the sessile preceded the common oak, which is found mainly in lowland areas and more in the south and east (Mitchell & Coombes, 1998). Also early to arrive were aspen and rowan.

The total complement of native trees was about 35, about 25 in Scotland (Table 1). Europe was unfortunate during the Ice Ages because the great mountain systems run from east to west. The flora and fauna were trapped between the northern ice and the mountain ice. The Mediterranean prevented access to Africa. In Canada and the northern USA, which experienced the same ice ages, the mountains run north to south.

Trees migrated southwards along mountains or valleys at their preferred climate, and afterwards migrated back again. Hence there is an immense wealth of species, broadleaved and coniferous, in North America. The National Park of the Appalachians, for example, possesses 131 native trees whereas the European figure is 85. Britain has two species of oak; the USA has 80. Britain was recolonised by species hardy enough to have survived on the European plains and sufficiently fast moving to migrate back in the 6000 years before the Channel was created.

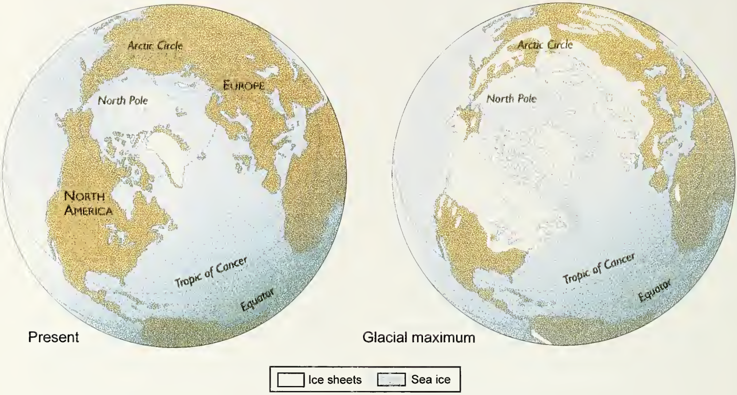
ISOCHRONE CONTOUR MAPS (FIGURES 6A AND 6B)

The maps show the history of the spread of some trees through these islands. During a warm early period the small-leaved lime (*Tilia cordata*) was dominant over large areas and the wych elm (*Ulmus glabra*) and bird cherry (*Prunus padus*) were other early arrivals. Ash (*Fraxinus excelsior*), field maple, yew and hawthorn arrived with time to spare, probably with wild cherry (*Prunus avium*) and crack willow. The land bridge was of chalk, and apart from holly and hornbeam, the last trees to cross it were those that thrive on chalk and are often now found wild only near chalk hills – the wild service tree, whitebeam, beech and, probably last, box. (Mitchell & Coombes, 1998.)

BRITAIN'S TREES C.6500 YEARS AGO (Figure 7)

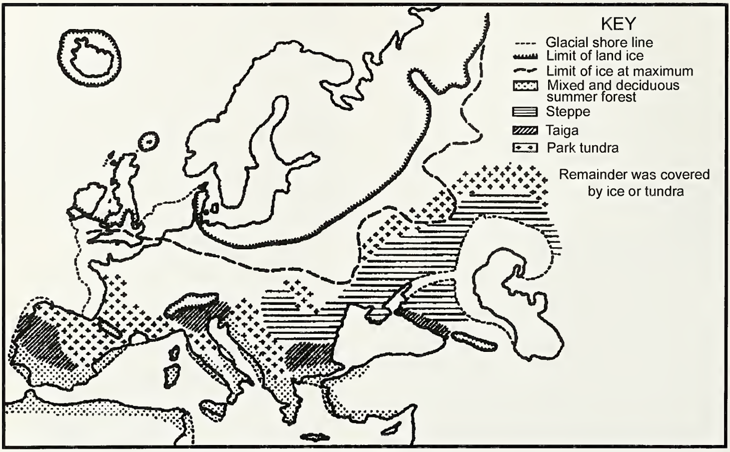
There is little evidence for Scots pine being a major component of central Scottish woodlands (Dickson et al., 2000). It was however the principal tree in the Highlands with tree birches and hazel dominating the Outer Hebrides and Northern Isles. By the time of maximum woodland expansion low lying, mainland Scotland north to the Great Glen was in the zone of oak dominance, with wych elm, alder and ash. Soil conditions determined woodland composition. Small amounts of Scots pine grew on drier areas of peat bog.

Figure 3. Ice sheets in the northern hemisphere



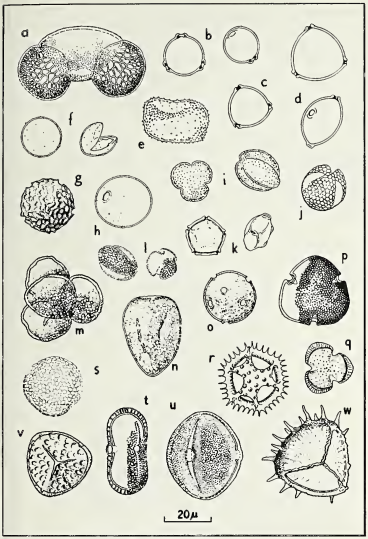
Source: Lamb & Sington, 1998

Figure 4. European vegetation at last ice glaciation



Source: Simms, 1990

Figure 5.



Drawings of pollen grains and spores frequently recognised in samples from British peats, lake muds and archaeological layers. a. Scots Pine, b. Tree Birch, c. Dwarf Birch, d. Hazel, e. Yew, f. Juniper, g. Wych Elm, h. Poaceae (Grasses), i. Oak, j. Ash, k. Alder, l. Willow, m. Heather, n. Cyperaceae (Sedges and related plants), o. Ribwort Plantain, p. Small-leaved Lime, q. Mugwort, r. Dandelion-type, s. Pondweed, Hogweed-type, u. Common Rock-rose, v. Bogmoss, w. Lesser Clubmoss. 1 micron = one thousandth of a mm. From Pigott and Pigott (1959)

Source: Dickson & Dickson, 2000

Table 1: British Native Tree Species

Bold = 15 species of natural woodlands.
Non-bold = species found in non-woodland habitats.(except *Arbutus*, wild now in Ireland, not in Britain)
*= not native in Scotland (Mitchell, 1974)

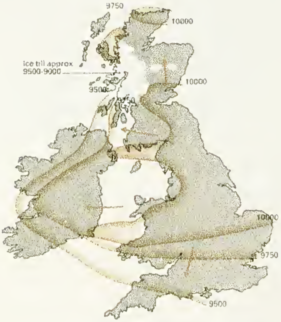
Alder (*Alnus glutinosa*)
Crab Apple (*Malus sylvestris*)
Ash (*Fraxinus excelsior*)
Aspen (*Populus tremula*)
***Beech (*Fagus sylvatica*)**
Silver Birch (*Betula pendula*)
Downy Birch (*Betula pubescens*)
Blackthorn (*Prunus spinosa*)
*Box (*Buxus sempervirens*)
Bird Cherry (*Prunus padus*)
Wild Cherry, Gean (*Prunus avium*)
Wych Elm (*Ulmus glabra*)
Hazel (*Corylus avellana*)
Hawthorn (*Crataegus monogyna*)
Holly (*Ilex aquifolium*)
***Hornbeam (*Carpinus betulus*)**
Juniper (*Juniperus communis*)
***Small-leaved Lime (*Tilia cordata*)**
Broad-leaved Lime (*Tilia platyphyllos*)
*Field Maple (*Acer campestre*)
Pedunculate Oak (*Quercus robur*)
Sessile Oak (*Quercus petraea*)
*Wild Pear (*Pyrus communis*)
Scots Pine (*Pinus sylvestris*)
Black Poplar (*Populus nigra*)
Rowan (*Sorbus aucuparia*)
***Wild Service Tree (*Sorbus torminalis*)**
*Strawberry Tree (*Arbutus unedo*)
*Whitebeam (*Sorbus aria*)
Almond Willow (*Salix triandra*) (probably not native to Scotland, Stace, 1997)
Bay Willow (*Salix pentandra*)
Crack Willow (*Salix fragilis*)
Goat Willow (*Salix caprea*)
White Willow (*Salix alba*)
Grey Sallow (*Salix cinerea*)
Yew (*Taxus baccata*)

Source: Miles, 1999

Figure 6a. Isochrone Contour Maps

Spread of tree species

Data from Prof. Birks of Bergen using radiocarbon dated pollen samples



Birch *(Betula pubescens* and *B. pendula)*

Hazel *(Corylus avellana)*

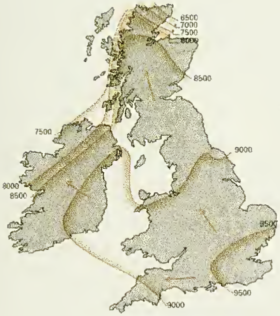
Pine *(Pinus sylvestris)*

Alder *(Alnus glutinosa)*

Source: Milner, 1992

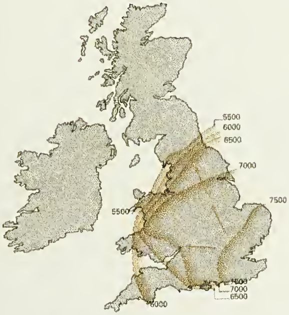
Figure 6b. Isochrone Contour Maps

Arrows give direction of spread.
Lines represent limit of spread at the date before present.



Elm *(Ulmus* species*)*

Oak *(Quercus* species*)*

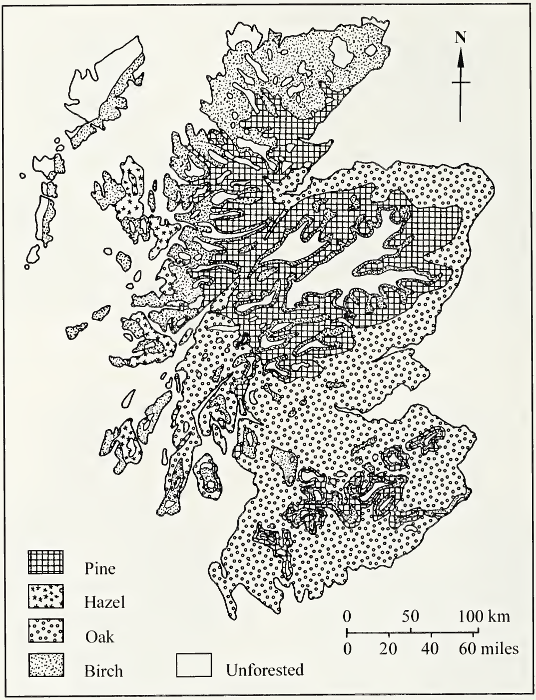


Lime *(Tilia cordata* and *T. platyphyllos)*

Ash *(Fagus sylvatica)*

Source: Milner, 1992

Figure 7. Woodland cover of Scotland several thousands of years ago, before woodland clearance had begun.



Source: Dickson & Dickson, 2000

Within a thousand years of the maximum a dramatic reduction in elm occurred, primarily a result of disease but possibly enhanced by human activity. Pollen analyses from Lenzie Moss, Lochend Loch bog and Drumpellier show that extensive woodland clearance took place before 2000 years ago by Iron Age pastoralists. During the last two thousand years woodlands have grown and declined as a result of variations in both climate and human activity.

NATURALISED TREES (Table 2)

The native tree flora conspicuously lacks a spruce, fir, larch, beech or maple (Scott, 2002); but examples of all of these have been introduced to Scotland and have shown themselves capable of natural regeneration.

Table 2: Naturalised Trees

Naturalised refers to an alien plant that has become self perpetuating (Stace, 1997)

a) Most common naturalised trees. Source: Milner, 1992

Several common trees that were introduced to these islands over the past few hundred years have since become naturalised. For instance, the Sycamore (*Acer pseudoplatanus*), which originated in central Europe, is now one of our most common trees, invading much of our scrub and woodland and growing vigorously as far north as the Shetlands and at altitudes of up to 460m. in mountain areas. The following is a list of the most common naturalised species, with their approximate dates of introduction:

Norway spruce *Picea abies* Native in last glacial period Reintroduced early 14th centurySweet chestnut *Castanea sativa* Introduced c. 100 AD
Sycamore*Acer pseudoplatanus*
Introduced c. 1250AD
Walnut *Juglans regia*
Introduced before 1000AD
White poplar *Populus alba* Early 14th century
Plane *Platanus orientali* 1350
Holm oak *Quercus ilex* 1580
Silver fir *Abies alba* 1603
Horse chestnut *Aesculus hippocastanum* 1616
European larch *Larix deciduas* 1620
False acacia *Robinia pseudoacacia* 1630

b) referred to as regenerating in 'The Changing Flora of Glasgow', 2000:

Laburnum *Laburnum anagyroides* 1560
Norway maple *Acer platanoides* 1638
Turkey oak *Quercus cerris* 1735
Grey alder *Alnus incana* 1780
Sitka spruce *Picea sitchensis* 1831
Lawson's cypress *Chamaecyparis lawsoniana* 1854
Balsam poplar *Populus trichocarpa* 1880
Ontario poplar *Populus candicans* ('Aurora') 1925
22 x willows
+ beech, hornbeam, field maple and lime (not native to Scotland but naturalised).

The dates of introduction are derived mainly from Wilkinson, 1981; also Campbell-Culver, 2001 and J. Dickson, pers. comm.

THE LAST 200 YEARS

The Gingko, a 'fossil' tree unaltered for 200 million years native to China, and Chile pine are examples of trees introduced in the 18th century. However the previous two centuries have seen an explosion in the number of tree species introduced to these islands as a result of the activities of the great plant hunters such as Menzies, Douglas, Fortune, Lobb, Forrest and Wilson.

Five of the more remarkable examples of conifer introductions are as follows. Three conifers from the Pacific North-west have grown to more than 200 feet in Britain: Sitka spruce, Douglas fir and grand fir.

Sitka Spruce.

Sitka spruce is regarded by foresters as the 'designer tree'. It has an extraordinary natural range of 1500 miles with uniform features. It is widely planted in poor, upland, acidic peat soils, where it can grow rapidly to produce a marketable stand of high quality timber from areas that are otherwise non-productive. It forms the most productive woods in the temperate world. Forest policy has introduced a random planting pattern of alternative species to replace the " serried ranks of conifers" so derided by conservationists.

Douglas fir.

The tallest 50 trees in the UK are Douglas firs and the tallest two are located in Glendaruel, Argyll and Moniack Glen, Beauly (Alderman, 2002).

The Grand Fir

The grand fir at Cairndow, Argyll was the first in the country to achieve 200 feet and for a while held the title of tallest tree in GB.

The Coastal Redwood.

The coastal redwood, *Sequoia sempervirens*, is the tallest tree in the world, found growing in the coastal fog belt of N. California. It survives up to 2000 years.

The Giant Sequoia

The giant Sequoia, *Sequoiadendron giganteum*, from the Sierra Nevada, has the biggest volume of any tree in the world. Within 80 years of its introduction in 1853 it was the biggest tree by volume in every county of GB. The largest are c.4000 years old. Both of these trees grow exceptionally well in our climate.

Many broadleaved trees have been introduced during this period but in height none of them remotely approaches that of champion conifers. Aesthetically however many of them surpass native species. Bright autumn tints distinguish introduced trees such as Japanese maples from the less bright natives. Furthermore the bark of species such as the Snake barked maple and Tibetan cherry is something to be marvelled at.

The 20th century has seen a reduction in the number of foreign trees being introduced but two may be mentioned:

The Dawn redwood, *Metasequoia glyptostroboides*, was known from Pliocene fossils when it was found in Hupeh province in 1941. Now there is one in most arboreta.

The Bristlecone pine, *Pinus aristata*, from the Rockies is closely related to *P. longaeva*, the oldest living tree at 5000 years.

THE CURRENT STATUS OF BRITISH NATIVE TREES

Most tree habitats in Britain have a long history of human interference and so it could be argued that there are no natural habitats left. Introduced specimens of a particular species bring alien pollen into the landscape and so pollute the native species. Many populations are only vaguely related to our original post-glacial trees. Small-leaved lime is the most researched species in this category. Isolated coppice stools are known that date back 2000 years. For hundreds of years the climate has not suited small-leaved lime particularly well but recent warm summers have encouraged the species to produce fertile seeds again (Gray & Grist, 2000). The native black poplar is very rare on account of the introduction of more productive hybrid timber trees (Miles, 1999). Willows are often adulterated by promiscuity, e.g. the grey willow (*Salix cinerea*) forms with other species three hybrids named in 'The Changing Flora of Glasgow' and five in the British Isles (Stace, 1997). Furthermore as many as 18 species of willow (including shrubs) may be found in Britain (Lusby, 2001). Imported beech and oak have caused considerable genetic pollution of existing trees. It has been argued that since common oak was better for shipbuilding purposes it was introduced to Scotland in preference to sessile oak with the result that much hybridisation with the local sessile species occurred.

MAN & NEW ECOSYSTEMS

Man has created entirely new ecosystems and some examples of these are as follows:

Heather Moorlands

Heather moorlands are largely an artifact (Gimingham, 1975). Along exposed coasts and at high altitude where trees compete poorly moors are natural. However the treeless tracts of heath that cover the Scottish highlands only appeared with the arrival of man and sheep grazing. Burning and grazing have prevented the heaths from returning to forest for thousands of years. With the decline in profitability of sheep grazing heath is being replanted with more profitable forests over much of its range. It is debatable whether this is a return to a natural state. Britain was heavily forested before the arrival of pastoralists. However burning and grazing for such a continuous length of time has arguably changed what is natural for these lands. On many heaths tree seed is so scarce that even when burning is halted and sheep removed forests do not immediately return. Many wild species have grown dependent upon these artificial ecosystems, including a number of endangered Arctic birds.

Chalk Fauna of the Downs

The unique chalk flora of the downs is an assemblage of light demanding plants that could never have flourished in the pre-settlement forests. This chalk and limestone grassland habitat possesses a wide variety of alkaline tolerant plants on the thin, dry and nutrient poor soils. The large blue butterfly is a species that requires wild thyme and ant grubs, *Myrmica sabuleti*, which rely on such close-cropped grasslands (Asher *et al*., 2001). Since the decimation of rabbits in the 1950's by the introduction of myxomatosis the grass has grown taller, the wild thyme and ants scarcer, and the butterfly is in trouble. Yet the rabbit was itself an alien introduction of mediaeval times; it was imported from the continent and kept for food and fur. So what is natural is debatable. Perhaps a landscape with alien rabbits and native blue butterflies or one without either.

Linear Features

Studies have found that many artificial linear features in the landscape - hedges, roadside verges and ditches, for example – often support a greater diversity of life than is found in the open countryside. Roadside vegetation serves as a breeding habitat for 20 of 50 native mammals, 40 of 200 birds, all 6 reptiles, 5 of 6 amphibians and 25 of 60 butterflies. Such vegetation also serves as corridors linking larger areas of wildlife habitat and so increase the chances of a species survival.

Agriculture

Agriculture has been practised for thousands of years. All the recent gains in production have come through technological improvement rather than clearing more land.

Timber

Some 75% of the total world production of commercial timber comes from temperate forests, almost entirely from lands that have been managed for sustained timber production for more than half a century. These plantations could meet the entire world's timber needs on a mere 5% of the area of all the world's existing forests.

ANIMAL BIODIVERSITY (KITCHENER, 1998)

There were two main causes of extinction of mammals since the end of the last Ice Age:

1. Climate change created new habitats where cold adapted species could no longer survive, e.g. reindeer
2. Human activity by a) hunting, e.g. polecat b) habitat destruction for agriculture e.g. lynx and c) hybridisation between native and introduced species.

Table 3 gives examples of other mammals that have become extinct since the last Ice Age.

Several large species were dependent on forest habitats, e.g. beaver, wolf, brown bear, lynx, wild pig and moose, but by the 18th century Scotland

Table 3: Extinction of land mammals in Scotland since the end of the last Ice Age.

Species	Date/Time when lost	Causes of extinction
Giant deer (*Megaloceros giganteus*)	?Mesolithic	C
Wild horse (*Equus ferus*)	?Mesolithic	C, ?X, ?K
Reindeer (*Rangifer tarandus*)	?Mesolithic	C
Auroch (*Bos primigenius*)	Bronze age (c. 3500 years ago)	?H, ?K
Moose (*Alces alces*)	Bronze age (c. 3500 years ago)	?H, ?P/K
Brown bear (*Ursus arctos*)	Roman times (or ?10th C. AD)	H, P/K
Beaver (*Castor fiber*)	c. 1550 AD	?K, ?H
Wild boar (*Sus scrofa*)	c. 1600 AD	?K, ?H, ?X
Wolf (*Canis lupus*)	1743 AD	P, ?H
Lynx (*Felis lynx*)	1770 AD	?H, ?P/K
Red Squirrel (*Sciurus vulgaris*)	c. 1800 AD	H, ?D
Polecat (*Mustela putorius*)	c. 1912 AD	P, ?K

Key: C – climate change; D – disease; H – habitat loss; K- hunting; P – persecution; X – hybridisation with domestic species.
Sources: Kitchener, 1998, 2001 and Humphrey & Quine, 2001

was amongst the most deforested countries in Europe. The large mammals had become extinct except for red deer which adapted to open moorland. Even the red squirrel may have become extinct. Most of today's population derives from introductions in the 18th and 19th centuries from England and Scandinavia. The red squirrel today may be declining because of its inability to digest acorns (Thomas, 2000). The acorns contain a digestive inhibitor that greys can ameliorate but reds cannot. Hence reds are more successful in conifer plantations where they feed on more nutritious pine seeds and where there are no oaks to give greys a competitive edge.

Bird extinctions have three main causes (Table 4):

Habitat loss. Wetland drainage has resulted in the loss of larger birds such as crane, bittern and white stork. The capercaillie became extinct as the Caledonian pine forest declined. It breeds in coniferous woodland from Norway to Siberia, with glacial relics in the Alps & Pyrenees. Birds of Swedish stock were re-introduced to Perthshire in 1837. From there they have colonised the E. Highlands and Loch Lomondside, where the islands contain amongst the highest densities in Scotland (Mitchell, 2001).

Hunting. The great auk, for example, was hunted to extinction. The last known British specimen was killed on Stac an Armin, St. Kilda, in 1840.

Persecution. Birds of prey suffered severe persecution from gamekeepers, sportsmen and farmers, e.g. osprey (returned to Scotland in 1954 to Loch Garten, eyrie built in Scots pine), goshawk, white-tailed sea eagle and red kite.

The overall temperature drop of each glaciation drove the bird population E, SE & S with the retreating vegetation. The birds returned N & W in a process that continues today. In the last 100 years > 20 species have thus extended their range. Yet > 50 species nest regularly in Britain but not in Ireland, a phenomenon not easily explained.

Mammal introductions: There are three main reasons for which mammals have been introduced (Table 5):

1. Aesthetic e.g. fallow deer
2. Accidental e.g. ship stowaways, such as rats; escapees such as rabbits
3. Sport e.g. sika deer, brown hares

Invertebrates and trees.

The number of invertebrates found on native trees is much greater than that found on introductions, although non-native conifer species appear to provide suitable habitat for a wide range of native fauna (and flora) (Humphrey & Quine, 2001). Some 500 species are associated with oak and 450 with the genus *Salix*. Most of these are insects, particularly moths and beetles. Of course rarity can be as important as sheer numbers, e.g. endangered species found on aspen are the aspen hover fly and the rare dark bordered beauty moth. The SWT hopes to create aspen corridors to keep these rare insects in existence.

Table 6 summarises gains and losses of mammals and birds since the last ice age.

The number of birds and mammals lost or gained is in itself less important than the effect of losses or introductions on the indigenous fauna. The absence of top mammalian carnivores causes much ecosystem imbalance such as an excess of deer leading to a lack of young trees. It has to be said that animal introductions have proved to be far more devastating than plant introductions.

Mink and water voles

The American mink was first brought to Britain in the late 1920's to be farmed for its fur. However it escaped into the wild in 1938, colonised successfully and is now implicated in the severe decline of the water vole (Kitchener, 1998).

Table 4. Extinction of birds in Scotland since the end of the last Ice Age.

Species	*Date of Extinction in Scotland (Date of Global Extinction)*	*Cause of Extinction.*
Bittern (*Botaurus stellaris*)	1830 AD	P
Osprey (*Pandion haliaetus*)	1916 AD	P
Sea Eagle (*Haliaeetus albicilla*)	1918 AD	P
Red Kite (*Milvus milvus*)	1884 AD ?1917 AD	P
Goshawk (*Accipiter gentilis*)	1883 AD	P
Capercaillie (*Tetrao urogallus*)	1785 AD	H, K
Spotted Crake (*Porzana porzana*)	1912 AD	H
White Stork (*Ciconia ciconia*)	1416 AD*	?H
Great Auk (*Pinguinus impennis*)	1840 AD (1844 AD)	K
Crane (*Grus grus*)	?	K, H
Great Bustard (*Otis tarda*)	16th C AD	?H, ?K
Great Spotted Woodpecker (*Dendrocopos major*)	1840-1850 AD	H

H = Habitat loss. K = Hunting. P = Persecution. Source: Kitchener, 1998.

Table 5. Introductions of land mammals to Scotland since the end of the last Ice Age.

Species	*Date of arrival AD*	*Purpose*	*Success (last record)*
Red-necked Wallaby (*Macropus rufogriseus*)	1975 AD	A	Y
American Mink (*Mustela vison*)	1938 AD	E	Y
Fallow Deer (*Dama dama*)	900 AD	K, A	Y
Sika Deer (Cervus nippon)	1870 AD	K, A	Y
Wapiti (*Cervus canadensis*)	1819 AD	K	N
White-tailed Deer (*Odocoelius virginianus*)	1832 AD	? K, ? A	N (1872)
Grey Squirrel (*Sciurus carolinensis*)	1892 AD	A	Y
Canadian Beaver (*Castor canadensis*)	1875 AD	A	N (1903)
Muskrat (*Ondatra zibethicus*)	1927 AD	E	N (1937)
Orkney Vole (*Microtus arvalis*)	3700 BC – 3400 BC	E	Y
House Mouse (*Mus domesticus*)	Iron Age	E	Y
Black Rat (*Rattus rattus*)	Iron Age or 1st C AD	E	N*
Brown Rat (*Rattus norvegicus*)	? 1730's; 1744-1754	E	Y
Rabbit (*Oryctolagus cuniculus*)	13th C	E	Y
Brown Hare (*Lepus europaeus*)	? 1st C	K	Y

A = Aesthetic. K = Hunting. E = Accidental .
N = No. Y = Yes. Source: Kitchener, 1998.
** excluding population on Shiants.*

Table 6: Birds & Land Mammals: Numbers of Species Gained and Lost Since End of the Last Ice Age in Scotland

Native Mammals extinct = 12
Re-introductions = 1
Net loss = 11

Native Birds extinct = 12
Re-colonisation & re-introduction = 7
Net loss = 5

Alien colonisations & introductions:
Mammals = 15 (4 unsuccessful) = 11
Birds = 44 (4 unsuccessful) = 40
Totals = 51

Net gains/(losses):	Mammals	Birds
Net gains	11	40
Net losses	11	5
Totals:	0	35

Sources: Summary of Tables 3, 4, 5 and, for bird introductions, Kitchener, 1998

The powan
The powan is a relict cold water fish confined to a few mountain lochs. In Loch Lomond the introduced ruffe is a significant predator of its eggs. So reserve stocks of this legally protected fish have been introduced to Loch Sloy and the Carron Reservoir (Mitchell, 2001).

The introduced NZ flatworm
The introduced NZ flatworm has a negative impact on native worms and is spreading rapidly.

Crayfish
The aggressive and invasive signal crayfish (*Pacifastacus leniusculus*) has almost wiped out the native white-clawed species (*Austropotamobius pallipes*) (Maitland *et al*., 2001).

Anyone wishing to discover more about the controversial topic of 'Alien species: friends or foes?', especially in a Scottish context, need look no further than the publication of the proceedings of the symposium about this topic held in 2001 to celebrate the Society's 150th anniversary.

Although this has been a wide ranging address, the world of micro-organisms has not been mentioned, but I hope to have demonstrated that whereas plant introductions have overall provided a welcome increase in this country's biodiversity animal introductions are proving to be far more controversial.

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